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Taxonomic Status of *Halipegus* spp. (Digenea: Derogenidae) Parasitic in the Mouth and Eustachian Tubes of North American and Mexican Amphibians

DONALD F. MCALPINE[1] AND MICHAEL D. B. BURT[2]

[1] Natural Sciences Department, New Brunswick Museum, 277 Douglas Avenue, Saint John, New Brunswick, Canada E2K 1E5 (e-mail: dmcalpin@nbnet.nb.ca) and

[2] Biology Department, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 6E1 (e-mail: huntsman@nbnet.nb.ca)

ABSTRACT: *Halipegus eccentricus* Thomas, 1939, and *H. amherstensis* Rankin, 1944, are shown to be junior synonyms, the latter only in part, of *H. occidualis* Stafford, 1905. The synonymy of *H. lermensis* Cabellero, 1941, with this latter species is also confirmed. Material redescribed as *H. occidualis* by Krull (1935) and *Cercaria sphaerula* Thomas, 1934, are shown to be junior synonyms of *Halipegus projecta* (Willey, 1930) n. comb. The type description for *H. amherstensis* Rankin, 1944, appears to be a composite based on specimens of *H. occidualis* and *H. projecta. Halipegus amherstensis* therefore becomes a junior synonym, in part, of *H. projecta* and, in part, of *H. occidualis.* We also review and correct reports of *Halipegus* spp. from North American and Mexican amphibians and indicate where continuing uncertainty exists.

KEY WORDS: amphibian, digenea, *Halipegus,* Mexico, North America, parasites.

Until recently, distinguishing the three North American species of *Halipegus* parasites in the mouths and eustachian tubes of frogs—*H. amherstensis* Rankin, 1944, *H. eccentricus* Thomas, 1939, and *H. occidualis* Stafford, 1905—has been considered impossible without reference to the morphology of the cercarial stage (Thomas, 1939; Rankin, 1944). However, as Goater (1989) has noted, since these digeneans mature in the mouth of the anuran definitive host and can be examined without killing the host, they offer unique opportunities for field studies that link host behavioral ecology with parasite population dynamics.

Using electrophoretic techniques, cercarial and adult morphology, and life history studies, Goater et al. (1990a, b) demonstrated that in *Rana clamitans,* worms they identified as *H. eccentricus* and *H. occidualis* showed a site fidelity that permits separation of these species—*H. eccentricus* being found in the eustachian tubes, *H. occidualis* being found under the tongue. They also confirmed subsequently that longer filaments project from the eggs of *H. occidualis* than from the eggs of *H. eccentricus.* These differences are in agreement with the description of *H. eccentricus* Thomas, 1939 (eustachian tube, egg filaments 56–58 μm), and the redescription of *H. occidualis* Stafford, 1905 (under tongue, egg filament 160–200 μm), provided by Krull (1935). Stafford (1900) first reported specimens he later described as *H. occidualis* as the European frog ear-fluke, *H. ovicaudatum,* and noted he had collected the worms from the eustachian tubes of Ontario bullfrogs. Later (Stafford 1905) when he described the material as new he reported the egg filaments as "about 56 μm" but does not mention the site of infection in the host. It is clear that the original description of Stafford (1905) for *H. occidualis* is based on material which is in agreement with the description of worms designated *H. eccentricus* by Thomas (1939). Here we attempt to resolve certain taxonomic problems this presents, review and correct reports of *Halipegus* spp. from North American and Mexican amphibians, and indicate where there is continuing uncertainty over the identity of some *Halipegus* material. Previously, McCauley and Pratt (1961) dealt with *Halipegus aspina* Ingles, 1936, described from the stomach of *Rana boyli* in California. They proposed the genus *Deropegus* to accommodate this worm and identified it as normally a parasite of salmonid fishes.

Materials and Methods

The following specimens were examined: *Halipegus amherstensis* Rankin, 1944: holotype plus two paratypes collected South Amherst, Massachusetts, from *Rana catesbeiana* (U.S. National Parasite Collection [USNPC] 36883); *Halipegus amherstensis* Rankin, 1944: 3 slides prepared by Cabellero (1947) in his redescription of this species, collected Xochimlco, Mexico, from *Rana montezumae* (Coleccion Helmintolo-

gica del Instituto, 22–13); *Halipegus eccentricus* Thomas, 1939: holotype and one immature collected Twin Lakes, Cheboygan County, Michigan, from *R. catesbeiana,* and one immature from *R. pipiens* tadpole infected experimentally from cyclops (USNPC 9203). Note: Thomas (1939) reports the type date as 2 July, 1933, but the type is labelled 1937; *Halipegus lermensis* Cabellero, 1941: single paratype collected in Lerma, Mexico, from *R. pipiens* or *R. montezumae* (USNPC 44988), plus an additional specimen identified by Cabellero (USNPC 87493); *Halipegus occidualis* Stafford, 1905: 20 vouchers collected by Brooks (1976) in Nebraska—18 from *R. catesbeiana* and 2 from *R. pipiens* (Harold W. Manter Laboratory, University of Nebraska State Museum, Lincoln [HWML] 20098–20102); and *Halipegus occidualis* Stafford, 1905: voucher reported as *Halipegus occidualis* sensu Krull (1935) by Russell and Wallace (1992) collected in northern Idaho from the eustachian tube of *R. pretiosa* (USNPC 81914).

Table 1. Comparison of morphometric features reported to separate *Cercaria projecta* Willey, 1930, and cercaria of *Halipegus occidualis* sensu Krull (1935). Means are in parentheses.

H. projecta	*H. occidualis*
Cercaria body 100–150 μm	Cercaria body 145–270 μm
Oral sucker; 20 μm	Oral sucker; 26–43 (33) μm
Ventral sucker; slightly larger than oral sucker	Ventral sucker; 22–53 (39) μm
Ceca extending almost to posterior end	Ceca extending to near posterior end
Cyst; 65–72 μm	Cyst; 72–83 (76) μm
Caudal appendage; 6 ridges	Caudal appendage; 4–6 (5) ridges
Delivery tube; 390–432 μm	Delivery tube; 420–470 (458) μm

Results and Discussion

Apparently no type specimens now exist for *H. occidualis.* However, because material described by Thomas (1939) as *H. eccentricus* is identical to that described by Stafford (1905) as *H. occidualis, H. eccentricus* Thomas, 1939, must be considered a junior synonym of *H. occidualis* Stafford, 1905. The cystophorous *Cercaria californiensis* described by Cort and Nichols (1920) from Lake Temescal, near Oakland, California, possesses the cercarial streamers reported for *H. eccentricus* by Thomas (1939). Thomas (1939) noted that these forms were "similar in many respects," and we can find nothing that distinguishes them from each other. However, as we also show here, there is uncertainty about the identity of several western North American *Halipegus* spp. or *Halipegus*-like worms. Although *C. californiensis* may indeed be a junior synonym of *H. occidualis,* we believe it is premature to synonymize these species until there is further study of the genus in western North America.

Material described as *H. lermensis* from Mexican *Rana montezumae* and *R. pipiens* by Cabellero (1941) was later (Rankin, 1944; Cabellero, 1947) regarded as a junior synonym of *H. occidualis.* The identity of the host is unclear. The *R. pipiens* complex includes more than 20 species (Hillis, 1988), but according to Flores-Villela (1993), *R. berlandieri* and *R. brownorum* are the only members of the complex in the area of the Yucatan Peninsula, near Lerma, where Cabellero (1941) collected his material. Cabellero (1941) reported that these worms were collected from the eustachian tubes of frogs and that egg filaments were 74–78 μm. It is difficult to get accurate measurements of filament lengths in *Halipegus* spp. when eggs are packed tightly in the uterus, as they are in the specimens we examined, but the two filaments we were able to measure were 58 μm and 63 μm. We are in agreement with Rankin (1944) and Cabellero (1947) that *Halipegus lermensis* is a junior synonym of *H. occidualis.*

It is clear that the specimens Krull (1935) used in his redescription of *H. occidualis* are different from those described by Stafford (1905). However, in describing his material, Krull noted similarities between it and *Cercaria projecta* of Willey (1930) collected from Henryville, Pennsylvania. On the basis of similarities between the rediae, Krull (1935) even went so far as to suggest that these might be identical species.

Krull (1935) distinguished his material from *C. projecta* on the basis of

> the presence of cuticular projections at the anterior end of the body, the larger size of the cercaria body and suckers, longer ceca, the apparent difference in excretory systems, the apparent absence of a connection between the excretory system and the tail structures, larger cyst, number of ridges on the handle of the cyst, longer length of the delivery tube, absence of attachment of oral sucker to base of coiled delivery tube, and absence of uniform coiling of cercaria body in cyst.

Although Krull's material was somewhat larger than that described by Willey (1930), there is usually overlap in size (Table 1), and other dif-

Table 2. Mollusk hosts recorded for North American *Halipegus* species.

Parasite	Mollusk host	Source*
Halipegus projecta	*Helisoma anceps*	Willey (1930)
	Planorbella trivolvis	Thomas (1934)
	H. anceps	Krull (1935)
	H. anceps	Esch et al. (1997)
	P. trivolvis	Schmidt and Fried (1997)
Halipegus occidualis	*Planorbella occidentale*	Cort and Nichols (1920)
	P. trivolvis, Physella gyrina, P. parkeri	Thomas (1939)
	P. gyrina, Physa sp.	Ameel et al. (1949)
	Physa sp.	Guilford (1961)
	P. trivolvis	Brooks (1976)
	P. gyrina	Esch et al. (1997)
Halipegus sp.	*P. trivolvis*	Macy et al. (1960)

* We have followed Burch (1989) for current nomenclature of mollusks, which is not necessarily the nomenclature that appears in these reports. The generic status of snails identified as *Physa* sp. in these reports is uncertain.

ferences are insignificant. The redescription of Krull (1935) is based largely on living material. He also provided some measurements of material fixed in 10% formalin, as well as stained and mounted specimens, noting that their smaller size is due to contraction. Willey (1930) does not state whether his measurements are based on living or preserved specimens. Other differences may be due to the manner in which material was handled and maintained in the laboratory (Krull noted that cercariae kept in clean water lived up to 2 weeks, while Willey kept his material alive more than 6 weeks under similar conditions) or the way in which observations were interpreted. The cuticular projections at the anterior end of the cercarial body reported by Krull (1935) are a good example. These projections, which are not present in the figures of Willey (1930) are considered diagnostic by Krull (1935). However, examination of the photographs of *Halipegus* cercaria in Goater et al. (1990a) suggests that it would be easy to interpret these projections as present or absent in material examined by light microscope. We therefore consider *H. occidualis* of Krull, *née* Stafford, 1905, a new species whose larval stage is *Cercaria projecta,* and we rename it *Halipegus projecta* (Willey, 1930) n. comb.

We also consider *Cercaria sphaerula* Thomas, 1934, collected from Mullet Lake, Michigan, a junior synonym of *C. projecta.* There appears to be nothing other than size distinguishing the two, a difference that could be due to development in different snail hosts. Thomas (1934) collected his material from the mollusk *Heliosoma trivolvis* (=*Planorbella trivolvis*), whereas Willey's specimens came from *H. antrosa* (=*H. anceps*). *Halipegus* spp. have been reported to use several species of pulmonate mollusks as intermediate hosts (Table 2).

Rankin (1944) described *H. amherstensis* on the basis of specimens collected from *R. catesbeiana* and *R. clamitans* from Massachusetts. *Halipegus amherstensis* was later reported from Mexico (Cabellero, 1947) but the material was reidentified subsequently as *H. lermensis* (=*H. occidualis*). The status of *H. amherstensis* reported from *R. esculenta* in Europe by Prudhoe and Bray (1982) is unknown. Russell and Wallace (1992) reported mistakenly that Bouchard (1951) collected *H. amherstensis* in Maine. Rankin (1944) reported that *H. amherstensis* used one of the intermediate snail hosts (*Physella gyrina*) reported by Thomas (1939) for *H. occidualis* and is found in the eustachian tubes of *R. clamitans* and *R. catesbeiana,* the same hosts of *H. occidualis.* Morphological differences between *H. amherstensis* and *H. occidualis* seem to be minor, except for egg filament lengths, which are reported as 120–170 μm, close to the egg filament lengths of *H. projecta* as reported by Krull (1935). We have examined the type series (USNPC 36883) of *H. amherstensis* and find that the egg filament lengths of this material are much shorter. The filaments we were able to measure were 53 μm, 55 μm, and 58 μm (paratype, slide 20), 52 μm (paratype, slide 21), and about 50 μm (holotype, slide 22). Filaments of the holotype are clearly of the short type, but they were either broken or packed so tightly that

we were unable to get precise measurements, even though some eggs were removed from the uterus. This suggests to us that these specimens are all *H. occidualis.* However, Rankin (1944, 1945) recovered *H. amherstensis* both from under the tongue and from the eustachian tube in natural and experimental infections. He also found some larval stages similar to *H. eccentricus* Thomas, 1939 (=*H. occidualis* Stafford, 1905), and others closer to *H. occidualis* Stafford, 1905, sensu Krull (1935) (=*H. projecta* (Willey, 1930)). However, we are unable to associate the cercarial stage illustrated by Rankin (1944) for *H. amherstensis* with either *H. eccentricus* Thomas, 1939, or *H. projecta.* Nonetheless, all other evidence indicates that the type description is a composite based on specimens of *H. occidualis* and *H. projecta. Halipegus amherstensis* Rankin, 1944, therefore becomes a junior synonym, in part, of *H. projecta* (Willey, 1930) and, in part, of *H. occidualis* Stafford, 1905.

Cabellero (1947) reported and redescribed *H. amherstensis* from *R. montezumae* from Xochimilco, Mexico. He does not indicate site of infection or provide measurements of egg filament length. We have examined the 3 slides in the series (Coleccion Helmintologica del Instituto, 22–13). All are labelled "trompo de eustaquio," and all eggs are of the short-filament type, indicating the material is *H. occidualis.* The identity of the host frog is, however, uncertain. Hillis et al. (1988) show frogs of both the Alpha and Beta species groups of the *R. pipiens* complex occupying the region of the Mexican plateau where collections were made.

Macy et al. (1960) described the adult of *H. occidualis* from the esophagus and upper stomach of the amphibians *R. aurora, Taricha granulosa,* and *Dicamptodon ensatus,* and its life cycle in *Helisoma subcrenatum* (=*Planorbella subcrenatum*) in northwestern Oregon. They report that cercariae are identical to those described by Krull (1935) (i.e., *H. projecta*), but the egg filament lengths in their material are noted as 61–100 μm. The identity of one of these hosts, *Dicamptodon ensatus,* is now unclear. Populations in the area are now assigned to either *D. copei* or *D. tenebrosus* (see Good, 1989). We believe the specific identity of the *Halipegus* studied by Macy et al. (1960) is in need of confirmation.

Brooks (1976) reported *H. occidualis* from the eustachian tube of *R. catesbeiana* and *R. pipiens* in Nebraska on the basis of the morphology of cercariae from *Helisoma trivolvis* (=*Planorbella trivolvis*). However, Brooks' (1976) vouchers (HWML 20098–20102) include some worms labelled as *H. eccentricus* and others as *H. occidualis.* We have examined 20 of these vouchers and find that 4 of those (2 from *R. catesbeiana,* 2 from *R. pipiens*) labelled as *H. occidualis* are of the long–egg filament type and therefore should be considered *H. projecta* (Willey, 1930), while the remaining 16, labelled *H. eccentricus* from *R. catesbeiana,* have a short egg filament and are therefore *H. occidualis* Stafford, 1905. Obviously, the report of Brooks (1976) includes both *Halipegus* species. We have also examined the Idaho specimens (USNPC 81914) from the eustachian tube of *R. pretiosa* reported as *H. occidualis* sensu Krull (1935) by Russell and Wallace (1992). Considering their location in the host and their egg filament lengths (53 μm, 60 μm, 65 μm), we have reidentified these specimens as *H. occidualis sensu* Stafford, 1905.

Given the work of Goater et al. (1990a, b) and the above discussion, it is evident that worms in the genus *Halipegus* found in the eustachian tubes of North American frogs, with egg filaments 53–65 μm long, should be referred to *H. occidualis* Stafford, 1905, and that *H. eccentricus* Thomas, 1939, *H. lermensis* Cabellero, 1941, and *H. amherstensis* Rankin, 1944, are junior synonyms, the last only in part. *Halipegus* collected from under the tongues of North American frogs, with egg filaments of 160–200 μm, should be referred to *H. projecta* (Willey, 1930), with *Cercaria sphaerula* Thomas, 1934, *H. occidualis sensu* Krull, 1935, and *H. amherstensis* Rankin, 1944, as junior synonyms—likewise, the last only in part.

We propose that *Halipegus* species in North America inhabiting the eustachian tubes should be referred to *H. occidualis* Stafford, 1905. This includes reports from *R. catesbeiana* in Arkansas (Rosen and Manis, 1976), Idaho (Russell and Wallace, 1992), Michigan (Thomas, 1939; Muzzall, 1991), Nebraska (Brooks, 1976), and New Brunswick (McAlpine and Burt, 1998); *R. clamitans* in Massachusetts (Nickerson, 1898; Rankin, 1944), Michigan (Thomas, 1939; Ameel et al., 1947, 1949; and Muzzall, 1991), North Carolina (Goater et al., 1989), Wisconsin (Guilford, 1961; Williams and Taft, 1980), and New Bruns-

wick (McAlpine and Burt, 1998); and *R. pipiens* in Michigan (Thomas, 1939), Wisconsin (Williams and Taft, 1980), Nebraska (Brooks, 1976), and New Brunswick (McAlpine and Burt, 1998).

Species of *Halipegus* recovered from under the tongue of North American frogs should be referred to *Halipegus projecta* (Willey, 1930); their hosts are *R. catesbeiana* in Nebraska (Brooks, 1976); *R. clamitans* in Maryland (Krull, 1935), North Carolina (Goater, 1989; Goater et al., 1989; Goater et al., 1990a; Goater et al., 1990b), Massachusetts (Rankin, 1944), and Wisconsin (Gilford, 1961).

Esch et al. (1997), and numerous authors cited therein, studied *Halipegus* in the molluscan hosts *Helisoma anceps* and *Physa gyrina* (=*Physella gyrina*) and the frog *Rana clamitans* at the same study site in North Carolina as Goater (1989). These authors were able to confirm the identity of their material using cercarial morphology or a combination of site specificity and the length of the egg polar filament. Worms they reported as *H. occidualis* are here assigned to *H. projecta.* Worms they identified as *H. eccentricus* now become *H. occidualis.* Walton (1951) reported *H. occidualis* from *Rana sphenocephala* in the United States with no supporting details, and it is therefore impossible to determine the specific identity of this material. Likewise, it is not possible to determine the specific identity of *Halipegus* sp. reported from *R. clamitans* in Michigan (Krull, 1935), *R. pretiosa* in Wyoming (Turner, 1958), or *R. pipiens* in Iowa (Ulmer, 1970). Bouchard (1951) reported *Halipegus* sp. from the eustachian tube and oral cavity of *R. clamitans, R. palustris,* and *R. septentrionalis* in Maine without indicating the site of infection in specific host species. Although *H. occidualis* would seem to be involved, it is not clear whether the eustachian tubes of all three hosts were infected, and it is likely that *H. projecta* was also present. On the basis of egg filament length, Jones (1956) assigned material to *H. occidualis* of Krull (1935, =*H. projecta*) but did not report the host or location of collection.

As noted above, the specific identity of *Halipegus* sp. from amphibians in some regions in western North America and Mexico remains unclear. We therefore recommend that investigators note as precisely as possible the site of infection in the amphibian host, report measurements of egg filament lengths, deposit vouchers of both parasite and host in a permanent collection, and, wherever possible, examine cercariae.

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